Luminous Organs of Fish Which Emit Light Indirectly YATA HANEDA¹

INTRODUCTION

THERE ARE MANY REPORTS of luminous fishes, all of which, in earlier days, were taken from the deep seas. Luminous organs were found on the sides of the bodies, on the barbels, or on the antennae. In outward appearance these fishes were strangely shaped and feebly developed, with soft bones and loose muscles, and it was assumed that such unusual fishes belonged exclusively to the deep-sea fauna.

The material examined was invariably dead and damaged. It might have been newly caught, or else had been preserved in formalin or in alcohol for an indefinite period.

There seems to be very little record of observations on living material, and only the morphology of the organs of these fishes was studied. The organs were never really understood, and were mistaken for sensory organs, electric organs, or secondary eyes, or they were simply referred to as eye-like organs.

In the early days bacteriological knowledge, especially knowledge of luminous bacteria, was not far advanced, and fish which became luminous after death as a result of contamination by saprophytic luminous bacteria were mistaken for true luminous fishes.

Recent advances in the study of these interesting problems of luminosity have shown that luminous fishes are not confined to the deep-sea fauna, but may be found among the fauna of the shallow and coastal waters of the sea, and that luminosity may be caused by luminous bacteria. Moreover these studies have revealed that luminous bacteria play an important role in the production of light in

some fishes by entering certain ducts possessed by these fishes, and there settling down to a symbiotic existence. Within the duct they are cultured and utilized as a source of light, the fish undergoing some modifications to create an organization within itself to display the light. Such an association between a fish and luminous bacteria constitutes what is known as luminous symbiosis.

Most known luminous fishes are found in deep oceanic waters and have on the surface of their heads or bodies, or on their barbels, or on their antennae, curious arrangements of luminous organs of varied shapes, sizes, and arrangements. For example the luminous sharks have on the side of their bodies simple, small luminous dots which consist of groups of luminous skin organs. The genera Stomias, Chauliodus, and Gonostomias also possess numerous luminous dots in the underlying skin in addition to their regular series of luminous organs. A Porichtys species has rows of many small luminous organs which follow the direction of the multiple lateral lines. A Pseudoscopelus species has numerous minute luminous organs arranged in indefinite rows of a characteristic shape. The lantern fishes (Myctophidae) possess fewer luminous organs, but these are pearl-like and are arranged symmetrically in a series on each side of the fishes. In some species of Lampanyctus, luminous scales may be present above or below the tail base. Luminous patches or ducts occur on the head of Diaphus or on the body of Lampanyctus species. The Sternoptychidae and Stomiatidae are characterized by highly developed luminous organs of a more complex structure, consisting of a luminous body, reflector, lens, and color fil-

¹Tokyo Jikeikai Medical College, Tokyo, Japan. Manuscript received January 26, 1949.

ter. In addition to the serial luminous organs on the body there may be luminous organs on the jaws and near the eye. The more complex postocular organ of the Stomiatidae is freely movable, and can be rolled inward when not required.

In the families Stomiatidae and Malacosteidae there is a barbel which, in *Diplolychnus*, is luminous at the end. In many other species, however, it is not certain whether this barbel is luminous or not.

Deep-sea angler fishes have a luminous antenna. Lamprotoxus has a closed loop of luminous tissue on each side of the body between the head and pelvic region, while in Eurypharynx and Saccopharynx there is a looped luminous organ which extends along each side of the dorsal fin as far as its posterior extremity, beginning either just behind the skull or just in front of the anterior extremity of the fin. There is a half-moonshaped luminous organ which is freely movable and which can be rolled inside situated below the eye in Anomalops. Photoblepharon can shut off the luminous part of the organ by lowering a black membrane which functions like an eyelid. A species of Dolichopteryx has a luminous organ on the ball of the eye in front of the lens. Monocentris japonicus has a pair of luminous organs on the end of the jaws. Some species of the families Gadidae and Macrouridae possess a luminous organ ventrally in front of the anus.

All of these mentioned luminous organs are of the direct emission type. That is, their luminescence is emitted directly from the source (the luminous body) and remains more or less concentrated or focused at one point without much diffusion.

Some luminous fishes show no outward peculiarities in structure or appearance and resemble ordinary non-luminous fish. This is because the luminous body lies inside the fish and cannot be seen. Before its light can be seen it must first be directed to a reflecting

surface within the body. The light is reflected to pass through a considerable lateroventral translucent area of lenticular muscles where it appears as a diffused bluish glow. This diffusion may be compared with the effect which a frosted or "opal" bulb of an electric lamp has in screening the glare of the incandescent filament and reducing it to a diffused glow. As far as is known this indirect emission type is confined to *Acropoma* and the Leiognathidae.

These fishes differ from other luminous fish in possessing unusually large luminous areas. In fact they utilize half the muscles of their complicated body structure for this purpose. Recently Kato (1947) discovered that Apogon marginatus Döderlein, belonging to the family Apogonidae, also possesses this same type of luminous organ.

I have made a study of luminous fishes since 1933, and have collected considerable material in Japan and in more southerly regions. Subsequent to 1937 I worked at the Palao Tropical Biological Station on several occasions during which I took the opportunity to visit the Philippine Islands, North Borneo, New Guinea, Celebes, Java, Sumatra, and Malay, where I collected many specimens of living luminous tropical fishes and observed their luminosity.

Acknowledgment: I wish to express my hearty thanks to Dr. S. Hatai, former Director of the Palao Tropical Biological Station and to Dr. Y. Tokugawa, Tokugawa Biological Institute. My thanks are also due to Mr. W. Birtwistle, former Director of the Fisheries Department of Singapore and Federated Malay States, who helped me in many ways during my stay in Singapore. I must express my sincere gratitude to Dr. D. J. Pletsch, Scientific & Technical Division, ESS, GHQ, SCAP, who assisted me in obtaining publication of this paper.

LUMINESCENCE IN Acropoma japonicum Material

Acropoma is a genus of fishes of the family

Acropomidae found in the Sea of Japan and the Philippine Sea. Two species are known: Acropoma japonicum Günther, and Acropoma philippinense Günther. Acropoma philippinense was found near the Philippine Islands by the "Challenger" at a depth of 82 to 102 fathoms. Acropoma japonicum is known as "Hotaru-jako" in Japan, and is considered there to be a single species.

I have examined a large number of these "Hotaru-jako" in a fresh condition and believe that there are two species (Haneda, 1939) but in the absence of confirmation of this belief by an ichthyologist, I refer to them as Type I and Type II (Figs. 1 and 2). They both occur in the southern Japan Sea as a mid-water dweller in a depth ranging from about 80 fms. to 200 fms. They are beautifully rose colored and attain a length 200 mm.

If these two types are examined in detail many differences are found, not only between their external characters, but also between their luminous organs. For example:

Type I is colored pale red dorsally, and whitish ventrally.

Type II is a beautiful purple-red dorsally, and ventrally is light purplish-red.

Both possess many chromatophores on the ventral sides but Type II possesses the greater number.

The scales of Type I are firmly fixed in the body, while in Type II they are extremely deciduous; for this reason it is very difficult to obtain in the public fish markets specimens of Type II with scales attached.

The anus in Type I is situated approximately under the third spiny ray of the dorsal fin, but in Type II it is situated below the hindmost edge of the end of the dorsal fin.

The anus in Type I is white and in Type II it is strongly black pigmented.

Type I is furnished with a pair of canine teeth which Type II lacks.

Type I occurs in water of about 80 fms. in depth, while Type II occurs in waters more than 100 fms. deep. They are very seldom taken together by trawling vessels.

The greatest difference, however, lies in the size of the U-shaped internal luminous gland. That of Type I is short, with the ends directed posteriorly; while that of Type II is much longer, with the free ends directed anteriorly.

These differences, I suggest, justify the creation of a second species, but I prefer to call the two kinds of fish Type I and Type II. I have examined many specimens of both types, as well as males and females of each type. The gonads of Type I are full in October and those of Type II from December to February. All ichthyologists have considered them to be the same species, *A. japonicum*, and Type II only a variety of Type I, but in my opinion each is a distinct species.

During the winter season they are caught by trawlers in the Gulf of Tosa off Shikoku Island, Japan, in depths varying from 80 to 200 fathoms, and there is no difficulty in obtaining specimens in the Mimase fish market near the city of Kōchi, Shikoku Island. During each of the winters of 1934 to 1940 I obtained many specimens in this fish market. In Mimase and Urado near Kōchi, they are called Hotaru-jako, meaning "the small firefly fish," or Kigane-jako, and the fishermen who catch them during the night are aware of the luminosity in their ventral regions, as are most of the ichthyologists, who state that the luminosity is due to the numerous small black points on the ventral surface of the body. These they consider are skin organs similar to those of the luminous sharks, but they do not describe their structure.

It was not until I had dissected many fresh specimens that I discovered the peculiar luminous organs established in them and perceived that the small black points which had been believed to be small luminous organs were nothing more than chromatophores.

The luminous organs consist of the following five components: a U-shaped luminous filiform body; an external opening of the canal of the luminous body; a reflector; a series of lenses; and a means of controlling the display of luminescence.

Luminous Organ of A. japonicum Type I (Fig. 1)

Luminous Gland-The luminous gland is

a whitish-yellow U-shaped filiform body, like a U-tube, lying flat and embedded in the muscles of the pectoral and ventral regions. Each "limb" of the tube is sealed at its end. The bend of the tube lies nearer the head than the closed ends of the "limbs" or filaments. This bent filament has an outer layer of longitudinally arranged fibers, an inner layer of circularly arranged fibers, and an innermost folded glandular epithelium, which surrounds a hollow duct or cavity. It is pierced on the

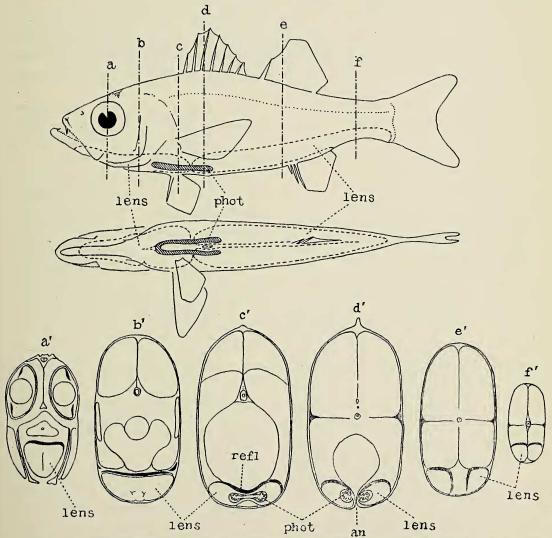


FIG. 1. Diagrammatic figure of the luminous organ of Acropoma japonicum Type I: phot, luminous gland; lens, lens; refl, reflector; a', b', c', d', e', f'—transverse sections at a, b, c, d, e, and f.

inner faces of the limbs by numerous capillary ducts which enter a larger central canal lying between the inner faces of the limbs of the U-tube. This canal is bounded dorsally and ventrally by concave membranes and has only one opening, which is at the anus. The whole luminous gland from a specimen 145 mm. long measured 14 mm., and from a fish 110 mm. measured 13 mm.

External Opening—In the gland, bacteria occur in the film of material which lies on the inner surface of the epithelial cells. These bacteria are present in clusters or else are attached to the surface of the gland cells. They pass from there into the duct or cavity of the U-shaped gland via the gland ducts. Here they remain until they pass through one of the numerous capillaries or pores into the larger central canal which opens in front of the anus. This is the only external opening of this canal. A luminous organ with an opening of this type is known as an open type of luminous organ.

Reflector—The reflector is a white, opalescent, opaque membrane lying above the luminous duct and extending from the isthmus to the end of the caudal peduncle. It lies rather low ventrally, and separates the lower ventral or keel muscles from the upper lateral and dorsal muscles. It passes below the pericardial and perivisceral cavities; under the latter it is depressed and forced downward into a concavity. Elsewhere it lies flat.

Lens Structure—The lower ventral or keel muscles below this membrane are lenticular and modified to transmit light. They are translucent but cloudy. They lie longitudinally and in pairs, i.e., one pair on each side. The first pair extends, one on each side, from the isthmus to the anus. The second pair lies, one on each side, from the anus to the end of the caudal peduncle. As they lie extended they may touch each other in places, but where they are not in contact they are separated by non-translucent muscle of ordinary structure. The luminous gland passes through

these muscles, and each limb passes backward, one on each side, the bend being in the anterior part of the body of the fish, and the closed ends of the limbs being directed backward in the direction of the anus. When I made complete cross sections of fresh fish. I noticed that where I had cut through the limbs of the organ, the luminosity was brilliant; it was only moderate and diffused in the muscles which were cut. The light was screened by the reflecting membrane above, but was reflected downward and laterally through the skin of the fish. Where I cut a cross section of a fish without cutting the limbs of the luminous gland, the muscles surrounding the limbs appeared to be luminous, suggesting that the muscles themselves were luminescent.

Light Control Mechanism—This luminous organ has in itself no regulating mechanism for controlling the display of light. On the other hand, the ventral area and lower lateral area below the reflecting membrane are furnished with a great number of chromatophores in the surface of the skin. Above the membrane this particular kind of chromatophore disappears and is replaced by another kind. The former are the chromatophores which at one time were considered to be the actual luminous organs, but by their contraction and expansion they probably control the amount of light emitted.

Luminous Organs of A. japonicum Type II (Fig. 2)

The luminous gland is situated in the ventral muscle and is long compared with that of Type I. It extends from the isthmus to about the 5th ray of the anal fin, where it bends with a short loop on each side of the fin. These loops are directed obliquely downward, and continue in a reverse direction for a short distance where the bend is continued to the center. In this way the two limbs form a kind of hooked loop, such as would be

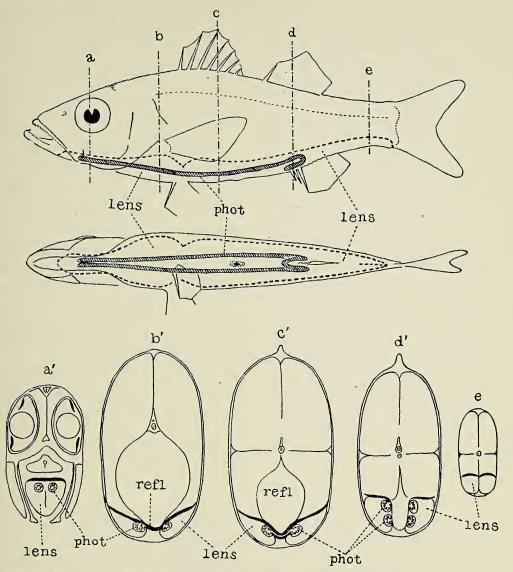


FIG. 2. Diagrammatic figure of the luminous organ of *Acropoma japonicum* Type II: phot, luminous gland; lens, lens; refl, reflector; a', b', c', d', e'—transverse sections at a, b, c, d, and e.

made if the closed end of a hairpin were bent over to form a hook.

The free ends of each limb of this organ lie in the isthmus, and the arrangement is a complete reversal of that found in Type I. The gland is reddish-yellow when fresh. Structurally it is similar to that described for the fish of Type I.

The central canal between the inner loops continues beyond the anus and opens into

the cloaca through an opening which completely encircles it.

The muscles which form the lenses are comparatively poor as lenses when compared with those of the Type I fish, but are similar in other respects and equally translucent. The chromatophores are extremely numerous in the ventral region, and there are many more of them than in the fish of Type I.

These two types of luminous organs of

Acropoma japonicum are peculiar organs of a new type. The luminous glands are situated in the muscles, and they may be considered as an indirect or reflecting type of luminous organ functioning by reflected light.

Remarks on the Luminescence

Since the luminous gland is not visible on the surface of the body, both types of fish, externally and in daylight, have the appearance of ordinary non-luminous fish.

In the dark, however, e.g., when caught alive in a net at night, the ventral area is brilliantly illuminated. The luminosity is continuous, never disappearing completely, but may be dimmed by means of the chromatophores.

When the fish are recently dead the luminosity persists in both types, but gradually becomes dim. One or two days after death the muscles become opaque and are no longer translucent, and then the luminosity is extremely dim. If, however, after this period, the luminous glands are removed it will be seen that their luminosity persists as brilliantly as before and can even be seen in daylight by shading the glands in the cupped hands.

Remarks on the Substance in the Luminous Glands

To examine the substance in the glands, I made emulsions of it in distilled water, in 0.5, 2, 3, and 4 per cent NaCl solutions, and in sea water. These emulsions were kept at 18°-23° C. and were examined in the dark.

The sea water emulsion was the most luminous; next in order were the 3 per cent NaCl, the 4 per cent NaCl, the 2 per cent NaCl (which was rather weak), and the 0.5 per cent NaCl (which was extremely weak). The distilled water emulsion was not luminous.

The temperature of the sea water emulsion was lowered to 0° C., at which temperature it showed only a weak luminescence, but recovered its strength when warmed to 18° to 23° C., within which range it was strongest. At temperatures above 30° C. the luminosity diminished until at 45° C. it was no longer visible. When cooled it regained its luminescence, but it was lost again below 0° C.; however, luminescence was again recovered when the emulsion was warmed.

The Luminous Bacteria

When the emulsion of the gland was ex-

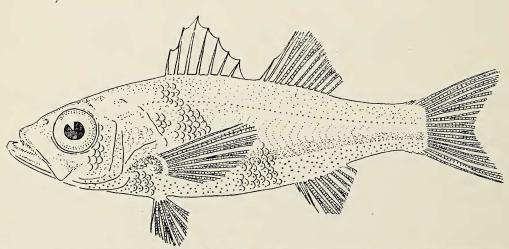


FIG. 3. Acropoma japonicum Günther Type I. The luminous organ is not seen externally, so that the fish looks like a common non-luminous one, but the lower part of the fish body is a lightning-like bluish-white color.

amined microscopically a large number of bacteria and some duct cell fragments could be seen. In the latter could be seen what were apparently bacteria since they stained well with Ziehl's solution and were Gram negative. Bacteria which had been taken from the luminous gland and cultured in media were tested for luminescence in the same solution as were the emulsions.

One hundred different strains of the luminous bacteria were obtained by the usual bacteriological techniques from 100 of each of the two different types of Acropoma japonicum. The cultures of bacteria taken from each of the types of fish showed some differences. On the basis of preliminary tests it appears that they represent two heretofore unknown species of bacteria which will be discussed at length in a separate paper. I tested the agglutination reactions of representative strains of these two new kinds of bacteria, and they showed a strain specificity similar to that of other symbiotic luminous bacteria (Kishitani 1930, 1932; Yasaki and Haneda, 1936).

LUMINESCENCE IN THE FAMILY LEIOGNATHIDAE

Material

The fishes belonging to the family Leiognathidae are true shallow-water forms, and are abundant in the southern Sea of Japan and in tropical seas. When I published my account of the luminescence of these fishes in 1940 I was not aware that their luminescence was already known, and it was only by chance that I found, in 1943, a reference to the work of J. W. Harmes in Biological Abstracts in the Raffles Museum Library. It is an abstract of a paper which appeared in 1928, entitled "Bau und Entwicklung eines eigenartigen Leuchtorganen bei Equula spec." Unfortunately I have not yet been able to see the full account of this discovery. However, while working independently on luminous organisms of the South Sea Islands at the Palao Tropical Biological Station, I discovered that *Gazza minuta* and several other species in this family are also luminescent when alive. The Leiognathidae living in shallow waters are not provided with externally visible luminous organs and superficially they resemble ordinary non-luminous fishes. For this reason their luminosity was unexpected.

Besides Gazza minuta I collected 15 other species of the Leiognathidae. Investigation of these species reveals that they all possess a luminous organ of a type similar to that of Gazza minuta.

Since the luminescence of these fishes of the family Leiognathidae was, I thought, unknown, I published the results of my investigations in 1940. I now present the results in revised form.

Gazza minuta occurs in clear water in Palao at a depth of about 30 meters and Leiognathus equulus lives in turbid water in the vicinity of mangrove trees at a depth of 1–2 meters. In Palao and Yap, L. equulus ranged in length from 60 to 70 mm.; in Ponape it was 180 mm. long; and in Sandakan, 200 mm. long. In Sandakan, the Chinese fishermen catch these fishes in nets and bring them every morning for sale in the Sandakan fish market.

In Japan there are three species, *L. argenteum* (Japanese name Uchi-Hiiragi), *L. rivulatum* (Oki-Hiiragi), and *L. elongatus* (Hime-Hiiragi).

L. argenteum and L. rivulatum are common on the southern coast of Japan. They are extremely abundant in Nagasaki where they are called Gira-gira or Gira. In Kōchi they are called Nirogi. In the bay of Urado near the city of Kōchi many old men may be seen fishing for Nirogi on any fine autumn day. L. argenteum is caught almost entirely by hook and line. This species lives in rather turbid water along the shores of the river estuaries, and it is from this fact that the

TABLE 1
Data on Collections of Luminous Leiognathidae

SPECIES	PLACE OF COLLECTION	DATE OF COLLECTION
Gazza minuta (Bloch) Koban-Hiiragi (Japanese) Kekek, Kekek labu (Malay)	Palao Yap Sandakan, B. N. Borneo Ponape Singapore Penang, Malay Batavia	June 1937, Feb. 1938 August 1937 March 1938 March 1940 March 1943, Nov. 1944 June 1943 March 1945
Secutor insidiator (Bloch)	Sandakan, B. N. Borneo	March 1938
Secutor ruconius (HamBuch.) Ukekuchi-Hiiragi (Japanese)	Sandakan Singapore, Penang Batavia	March 1938 June 1943 March 1945
Leiognathus equulus (Forsk) Seitaka-Hiiragi (Japanese) Kekek gadabang (Malay)	Palao, Yap Truk Ponape Sandakan Itoman, Okinawa Singapore, Penang Batavia	June, Aug. 1937; Feb. 193 March 1940 March 1940 March 1938 March 1938 June 1943, Aug. 1944 March 1945
L. fasciatus (Lacép.)	Palao Ponape Truk Sandakan Singapore	June 1937, Feb. 1938 March 1940 March 1940 March 1938 Sept. 1943
L. lineolatus (Cuvier & Valenciennes) Ito-Hiiragi (Japanese)	Palao Palao Palao	Oct. 1937 March 1940 Oct. 1943
L. splendens (Cuvier) L. daura (Cuvier & Valenciennes) L. bindus (Cuvier & Valenciennes) L. berbis (Valenciennes) L. dussumieri (Cuvier & Valenciennes) L. stercorarius Evermann & Seale	Sandakan Singapore Sandakan Singapore Davao, Philippines Singapore Singapore Singapore	March 1938 Sept. 1943 March 1938 Oct. 1944 Aug. 1939 Nov. 1943 Oct. 1944 Nov. 1944
L. elongatus Günther Hime-Hiiragi (Japanese)	Izu, Japan	Oct. 1938
L. rivulatum (Temminck & Schlegel) Uchi-Hiiragi (Japanese)	Tosa, Japan	Oct. 1939
L. argenteum (Lacépede) Oki-Hiiragi (Japanese)	Tosa, Japan	Oct. 1939

species derives its name of Uchi Nirogi—inshore nirogi. It is always present in the street markets. *L. rivulatum* occurs in the off-shore waters, and is taken only in nets. It is plentiful in the Mimase fish market near the city of Kōchi. Both species are usually dried for

sale, and are very good to eat.

L. elongatus is not common. It is also an off-shore species. I obtained my specimens off Suzukawa–Shizuoka Prefecture.

From the Itoman market, Ryukyu Islands, I obtained two specimens of L. equulus and

Gazza minuta. Both specimens were the same as those found in tropical seas.

In 1943–1944 I collected in Singapore the species as listed in the accompanying table.

Around Singapore and the Malay Peninsula these kinds of fishes are easily obtained in all seasons from the fishing trap known as the Kelong. Fowler (1938) reported 12 species of this family in Malaya.

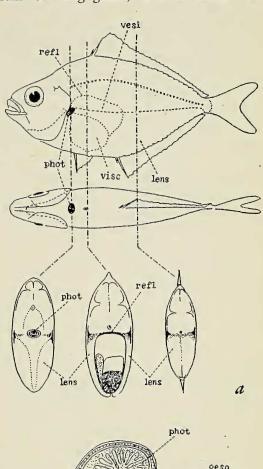
The Luminous Organ

Gazza minuta: Externally this fish does not present any unusual features, and it was only by a careful observation of the living fish by night that the bluish-white luminescence of the lower half of the body was revealed.

The source of the luminescence is a swollen ring of gland-like substance which encircles the oesophagus. It is covered with a white membrane except at two points, one located dorsally and the other ventrally. These appear as two small bean-shaped areas of a yellowish-white color. The ring contains a gland which has two openings (Fig. 4, op) which lead into the oesophagus.

The swim bladder and the thoracic and ventral muscles are so modified as to increase the efficiency of the light-producing mechanism. The swim bladder is lined with a remarkably bright silvery reflecting surface and the muscles of the thorax and the ventral parts of the body are translucent but somewhat cloudy. The swim bladder has no reflecting surface at its posterior end, which is translucent. Part of the dorsal silver lining is continued under the spinal column and acts as a reflector for the light which is transmitted backward through the translucent end of the bladder. Light is emitted from the two bean-shaped areas only, the dorsal one illuminating the swim bladder, the ventral one the thoracic and ventral muscles.

If the diagram of the longitudinal section of the fish through the swim bladder is studied, it will be seen that the anterior end of the swim bladder forms a parabola, and that a bean-shaped light spot (one part of the luminous ring gland) is at its focus. We



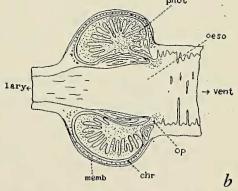


FIG. 4. a, Diagrammatic figure of the luminous organ of Gazza minuta (Bloch). b, Longitudinal section of the luminous gland of Gazza minuta (Bloch): phot, luminous gland; refl, reflector; lens, lens; visc, internal organ; vesi, swim bladder; chr, chromatophore; memb, membrane; op, opening of luminous gland; oeso, oesophagus; lary, larynx; vent, stomach.

have, in fact, a remarkably efficient parabolic reflector which reflects the emitted light backward even as far as the muscles of the caudal peduncle.

The ventral light spot directs its light downward, and, because of the cloudy translucent muscles of the thorax and abdomen, a diffused luminescence is seen in this area. Because of the presence of a white opaque membrane extending dorsally from the upper borders of the abdominal muscles of both sides, no light reaches the dorsal part of the body.

The bean-shaped areas are furnished with chromatophores, and it is perhaps due to their expansion that the light can be shut off, and by their contraction displayed. Possibly the white membrane which covers the ring can be contracted to cover the light spots, but this I was unable to confirm. Normally it is expanded to uncover them.

The complete luminous organ therefore consists of three components, possibly four: (1) the luminous ring gland; (2) the reflector; and (3) the lenses; with possibly (4), a shutter for the light spots which may be opened or closed either by the chromatophores or by the white covering membrane of the ring working independently or simultaneously with the chromatophores. In recently dead specimens these spots are closed by the membrane, but the gland material is still luminous.

As previously stated this fish differs from other luminous fish by its unusually large luminous area, utilizing in fact half the muscles of its extremely complicated body structure. The luminous glands are situated in the body, and may be considered to be of an indirect or reflecting type, functioning by reflected light in the same way as described for *Acropoma japonicum*; but *Gazza minuta* is not only provided with a membrane and chromatophores for displaying its luminescence, it has a far more complex luminous organ than *Acropoma japonicum*.

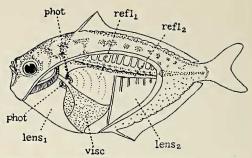


FIG. 5. Diagrammatic figure of the luminous crgan of Secutor insidiator: phot, luminous gland; refl₁, refl₂, reflectors; lens₁, lens₂, lenses; visc, internal organs.

Secutor spp.: Secutor insidiator (Fig. 5) and S. ruconius are luminous Leiognathidae, similar to Gazza minuta, but possessing a relatively larger luminous gland than does G. minuta. It is yellow in fresh material instead of white as in G. minuta.

The reflector is very efficiently arranged and is lined with a bright glossy surface.

The ventral muscles are cloudy and translucent. The ventral cavity walls are extremely thin and, because of this, its luminosity is greater than that of any of the other members of the family Leiognathidae.

Leiognathus spp.: There are many species of Leiognathus, varying in length from 50 mm. to 200 mm. With the exception of the male L. rivulatum they have comparatively small luminous glands. Even when compared with Gazza and Secutor, this has a comparatively small luminous body and thick ventral cavity walls, which are only moderately translucent, thus diminishing the brightness of the luminosity.

The species L. equulus, L. fasciatus, L. splendens, L. lineolatus, L. bindus, L. berbis, L. argenteum, L. dussumieri, L. stercorarius, and L. daura are also only moderately luminous. There is an interesting feature of the Japanese species, L. rivulatum, viz.: the luminous gland of the male is either very large or else very small. I am of the opinion, though by no means certain, that this differ-

ence in size is due to age. The luminous gland of the female is smaller and the luminosity of the female is therefore very weak compared with that of the male.

The luminous gland of L. rivulatum differs from that of all other Leiognathidae in that it does not surround the oesophagus completely, but occurs as an external swelling on the dorsal part only.

L. elongatus also possesses a very small luminous gland with a poor reflector; in consequence its luminosity is feeble.

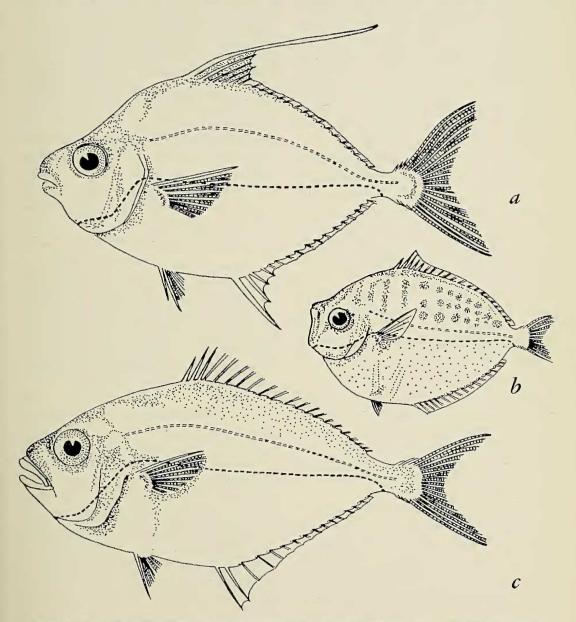


FIG. 6. a, Leiognathus equulus (Forsk.); b, Secutor insidiator (Bloch); c, Gazza minuta (Bloch). The luminous organs are not seen externally, so that the fish look like common non-luminous fishes, but the lower half of these fish bodies, namely, the parts below the black lines, are a lightning-like bluish-white color.

Remarks on the Luminescence

A specimen of Gazza minuta and one of Secutor insidiator were put into a tank of sea water in a dark room and their luminescence was studied. No luminescence could be seen when the fish were viewed dorsally, but if they were viewed laterally a diffuse bluish-white luminosity could be seen. If the area where the transparent scales are arranged was examined directly or obliquely from below, a faint bluish light was seen, emanating from the chest, thorax, abdomen, and tail areas. The light showed uninterruptedly in these areas. It did not shine brilliantly, but was feeble and diffused.

If the fish received a strong stimulus or was removed from the water, the lower part of the body lighted up brilliantly, most strongly in the thoracic and abdominal regions. This sudden increase in brilliancy was accompanied by a croaking sound, the production of which is a peculiarity of the Leiognathidae.

If during this brief period of maximum brilliancy the fish was enveloped in a cellophane wrapper and was laid on a photographic film, it would produce a bright image.

After death the luminous gland was surrounded by the membrane and the light was no longer visible, but if the fish was dissected and the membrane covering the gland was removed, this membrane was found to be luminous and, when kept in an ice box at 5–10° C., it remained so for 2 days.

Contents of the Luminous Gland

When the substance of the luminous gland is freshly made up as a 3 per cent salt emulsion, the whole of the emulsion will be luminescent, but if it is allowed to stand, only the upper layer exposed to the atmosphere will glow while the deeper lower layer becomes non-luminous. When shaken up in air the whole emulsion becomes luminous again.

Luminescence is greatest at a temperature of 26°-30° C. in the tropics (in Japan at about 20° C.) and becomes feeble at 4° C. When the temperature is raised, it increases and finally disappears at 45° C., but after once attaining this latter temperature it fails to recover its luminosity even when cooled again. An emulsion in nearly 3 per cent NaCl gives the best results; an emulsion in distilled water produces no light. If such a distilled-water emulsion is centrifuged the upper clear solution is non-luminous but the sediment is luminous. Microscopically this emulsion is made up of disintegrated particles of gland cells with innumerable bacteria, and it appears from the results of these experiments that the contents of the luminous gland consist of luminous bacteria. In order to test this, isolation experiments were carried out to cultivate them in a 3 per cent NaCl agar-agar culture medium.

Culture of the Luminous Bacteria

A pure culture of the luminous bacteria from the luminous glands was prepared by the usual bacteriological techniques. After 8–10 hours a small, round, transparent and luminous colony appeared. From this start a pure culture which was free from any contaminating bacteria was obtained.

It was clearly demonstrated that the same kind of fishes always had the same kind of luminous bacteria and that the Leiognathidae of the tropical sea and those of Japan possessed luminous bacteria of the same group, with only slight variations probably due to the effects of temperature. There is a curious feature, viz., the bacteria in culture are not as brilliant as are those in the gland, probably because of the unsuitability of the medium for greatest luminosity. The details of the bacteriological work will be presented elsewhere.

SUMMARY

Some luminous fishes show no outward peculiarities in structure or appearance and

resemble ordinary non-luminous fish. This is because the luminous body lies inside the fish and cannot be seen from outside.

These fishes differ from other luminous fishes by their unusually large luminous areas, which utilize as much as one half or one third of the muscles of the extremely complicated body structure of the fish.

The luminous fishes hitherto known are provided with a direct radiating luminous organ, while the fishes described in this paper possess an indirect radiating luminous organ. These organs of indirect emission are peculiar organs of a novel type, which appear to be confined to *Acropoma* species, the Leiognathidae, and *Apogon marginatus* Döderlein.

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